

Noise-enhanced transmission of spike trains in the neuron

X. GODIVIER and F. CHAPEAU-BLONDEAU(*)

*Équipe Signaux Systèmes et Applications, Faculté des Sciences, Université d'Angers
2 Boulevard Lavoisier, 49000 Angers, France*

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Abstract. – We consider the transmission of spike trains in a conductance-based neuron model. A superposition of periodic coherent trains impinge on the neuron, but in a number that is too small to trigger an output response. We then show that addition of incoherent noise trains on the input allows a neuron response exhibiting correlation with the coherent input trains. Furthermore, the number of noise inputs can be increased up to an optimal value where the coherent part of the response reaches a maximum. This property of noise-enhanced signal transmission can be related to the phenomenon of stochastic resonance. The present study demonstrates for the first time the possibility of stochastic resonance in a realistic situation of multiple spike train transmission by the neurons, and it assigns a useful role in information processing to spontaneous random neuron spiking.

Introduction. – Some fifteen years ago, in the context of climate dynamics, a paradoxical nonlinear effect has been discovered, under the name of stochastic resonance [1], [2]. This effect can be described as an enhancement of the transmission of a coherent signal by certain nonlinear systems, that is obtained through an increase of the noise applied to the system. This property has since been observed in a wide range of both model systems and natural ones, including electronic circuits, ring lasers, superconducting devices, and neurons [3], [4].

For the neuron, stochastic resonance has been found in various theoretical models [5]-[9]. Also, experimental demonstrations have been obtained on hair mechanoreceptor neural cells of the crayfish [10] and of the cricket [11]. All these studies have considered the case of a peripheral sensory neuron, that is submitted to a pair of analog signals which are a direct image of analog stimuli from the external world to which the sensory neuron is directly exposed. Usually, one of these signals is a sinewave and the other a continuous Gaussian noise. Stochastic resonance is

(*) E-mail: chapeauuniv-angers.fr.

then observed in the transmission of the analog stimulus when the power of the noise signal is increased. Another recent study displaces the focus from the individual neuron to a complete neural system [12], and demonstrates (both with computational and experimental results) stochastic resonance in weak visual stimulations in the central receptive field as affected by noise in the surrounding field.

Beyond the case of these peripheral sensory neurons which are submitted to analog stimuli because of their direct contact with the external world, it is known that most neurons process signals under the form of trains of spikes. The possibility of stochastic resonance in spike train transmission was first established in [13], with a simple integrate-and-fire neuron model submitted to one coherent train and one noise train. To progress toward a more realistic assessment of stochastic resonance in the neuron, one especially has to recognize that a neuron response is usually conditioned by many more than two inputs. We investigate here the possibility of a stochastic resonance effect with multiple spike trains (both coherent trains and noise trains) applied to a neuron. Our investigation considers a more realistic conductance-based model for the neuron and the synaptic transmission, and a special care is devoted to attributing plausible values to the neural parameters, rather than values that are *ad hoc* to observe stochastic resonance. The present study is the first to examine whether and how stochastic resonance in spike train transmission can take place, in the realistic situation where many (hundreds of) trains condition the neuron response. We show that a new scheme can be devised where an increase in the number of noise trains onto the neuron can result in an improvement of the transmission of the coherent trains.

Stochastic resonance in spike transmission. – In neural signal transmission, a presynaptic action potential (spike) produces the rapid release of the neurotransmitter in the synaptic cleft, that in turn triggers ion channels which induce changes in the electric conductance of the membrane at the postsynaptic region. The resulting evolution of the membrane conductance $G_i(t)$ in a synaptic region i of a neuron can be modelled as [14]

$$\frac{dG_i}{dt} = -\frac{G_i(t)}{\tau_G} + [G_i^{\text{sat}} - G_i(t)]w_i E_i(t), \quad (1)$$

where $E_i(t) = \sum_k \delta(t - t_k)$ represents the input spike train (with dimension s^{-1}) on the synaptic region i , τ_G is a time constant for the ion channel kinetics, G_i^{sat} is the saturation value of the synaptic conductance that arises from the finite number of postsynaptic channels, and w_i models the efficacy of synapse i in transducing input spikes into membrane conductance changes.

With several synaptic inputs on the neuron, its membrane potential $V(t)$ above rest evolves according to

$$C_m \frac{dV}{dt} = -G_m V(t) + \sum_i G_i(t)[V_i^{\text{rev}} - V(t)], \quad (2)$$

where C_m and G_m are, respectively, the membrane capacitance and conductance of the postsynaptic neuron at rest, and V_i^{rev} is the reversal potential of synapse i .

If the membrane potential $V(t)$ reaches the threshold V_{th} , an output spike is fired by the neuron. $V(t)$ is then reset to zero where it remains frozen during a refractory period T_r , after which the variation of $V(t)$ resumes according to eq. (2). The signal $S(t)$ on the neuron output thus evolves according to the following:

$$\begin{aligned} \text{if } V(t) = V_{\text{th}}, \quad & \text{then } S(t) = \delta(t' - t), \\ & V(t) \leftarrow 0 \quad \text{frozen during } T_r; \\ \text{else } & S(t) = 0. \end{aligned} \quad (3)$$

We now consider the response of the neuron when submitted to a superposition of $N_c + N_n$ input spike trains. A number N_c of these spike trains are coherent trains: they are periodic with period T_c , with the same period but a random phase for every coherent train. In other words, for i belonging to the N_c coherent trains, one has $E_i(t) = \sum_{m=-\infty}^{+\infty} \delta(t - mT_c + \varphi_i)$, where φ_i is a fixed phase for input train i that can fall anywhere, with uniform probability, between 0 and T_c . These coherent inputs can be viewed as the image of a periodic coherent stimulus received by a set of sensory receptors. The periodic stimulus impinges on the receptors with a distribution in its phase, and also the multiple neural pathways connect the receptors to the neuron under consideration may vary in length and delay. These elements justify the phase differences among the N_c coherent inputs.

The neuron also receives a number N_n of incoherent spike trains. These incoherent trains have no relation with the periodic coherent stimulus. They have their origin in random activities of neurons that can spontaneously emit a few spikes per second. Such spike trains have the status of a noise, that is assumed Poisson. In other words, for i belonging to the N_n noise trains, one has $E_i(t) = \sum_k \delta(t - t_k)$, where the t_k 's are Poisson random times, independent for different i 's, but with a common density $1/T_n$ of a few spikes per second.

We shall now show that when the coherent part of the input to the neuron is weak and cannot be acted upon (small external stimulus), a reinforcement of the noise part of the input can enhance the coherent response on the output at frequency $1/T_c$. This is properly the phenomenon of stochastic resonance.

The neuron model of eqs. (1)-(3) has been numerically simulated, with an Euler discretization of the equations, with a time step much smaller than the model time constants. Realistic numerical values, at least in order of magnitude, have been assigned to all the neural parameters [14]. We took $\tau_G = 3$ ms, $G_m = 10$ nS, $C_m = 100$ pF and $V_{th} = 20$ mV above rest. We considered only the presence of excitatory inputs with, for all of them, $V_i^{rev} = 70$ mV above rest. The saturation synaptic conductance is $G_i^{sat} = 2$ nS, the same for all synapses in order to limit the number of parameters. The synaptic efficacy also has the same value for all inputs, and is estimated to be $w_i = 0.7$; this value of w_i is consistent with estimations that can be deduced from underlying biophysical mechanisms of synaptic transmission [14], and it results in several hundreds of inputs that are typically needed to make the neuron fire. The coherent period T_c as well as the noise mean interspike time T_n are taken to be 500 ms. We emphasize that the present values are merely illustrative, and are in no way critical for the observation of the stochastic resonance effect, that is preserved over a wide range of parameter values.

In standard stochastic resonance, the coherent input alone is insufficient by itself to trigger the output, and it requires assistance from the noise. To conform with this condition, we chose a number $N_c = 250$ coherent inputs, that are insufficient by themselves to bring the postsynaptic neuron to fire. Noise inputs are then gradually added, through the lifting of some upstream inhibition. When their number N_n becomes sufficient, the neuron will start to fire. At first, the output firing will be rare, but it will be correlated with the coherent input spikes, since with N_n still small, firing requires a cooperative action of the coherent inputs and the noise inputs. As the number N_n of noise inputs is increased, the probability of output firing will gradually rise, reinforcing the content in the output which is correlated with the coherent input. As N_n is further increased, the noise trains alone will become sufficient to trigger the output, with no assistance from the coherent inputs. From then on, with increasing N_n , the correlation of the output with the coherent inputs will gradually diminish.

This nonmonotonic action of the noise has been precisely quantified through the computation of the output autocorrelation function $R_{SS}(\tau) \equiv \langle S(t)S(t+\tau) \rangle$, where $\langle \cdot \rangle$ denotes a time average over t . In general, as illustrated in fig. 1, $R_{SS}(\tau)$ contains a periodic component at the period T_c of the coherent inputs, superposed to a contribution from the noise, and the

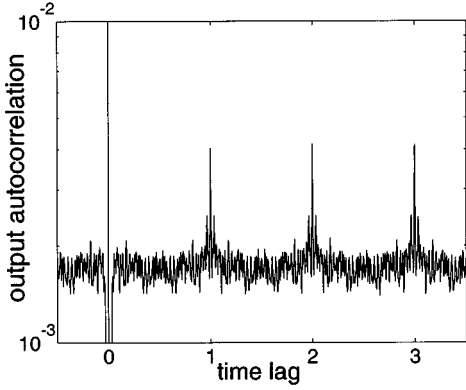


Fig. 1.

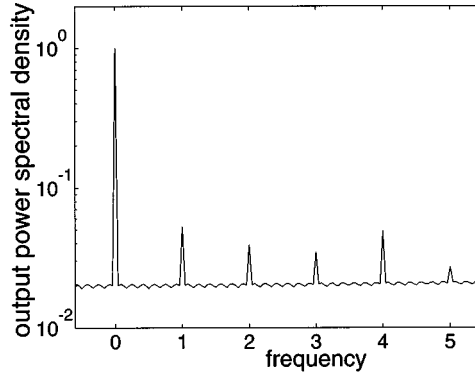


Fig. 2.

Fig. 1. – Typical normalized output autocorrelation function $R_{SS}(\tau)$ for the neuron, as a function of the time lag τ/T_c .

Fig. 2. – Typical normalized output power spectral density $P_{SS}(\nu)$ resulting from a Fourier transform of the autocorrelation of fig. 1, as a function of the frequency $\nu/(1/T_c)$.

relative importance of the coherent component displays the previously described nonmonotonic evolution with the amount of input noise. This can be properly quantified with the computation of the output power spectral density $P_{SS}(\nu)$, the Fourier transform of $R_{SS}(\tau)$. In general, as depicted in fig. 2, $P_{SS}(\nu)$ contains sharp spectral lines at integer multiple of the coherent frequency $1/T_c$, superposed to a broad-band continuous background due to the noise. In $P_{SS}(\nu)$, at the fundamental frequency $1/T_c$, the height of the coherent spectral line above the noise background, divided by the magnitude of this background, offers a standard definition for the output signal-to-noise ratio SNR [4]. We then study the variation of the SNR as a function of the number N_n of noise input trains applied to the neuron. This variation is shown in fig. 3, and it presents the nonmonotonic influence of the amount of input noise that is characteristic of stochastic resonance.

The curve of fig. 3 demonstrates that, with a small number of coherent inputs at period T_c which are insufficient to trigger the neuron, addition of noise inputs allows a neuron response exhibiting correlation with the coherent inputs. Furthermore, the number of noise inputs can be increased up to an optimal value where the coherent part of the response, at frequency $1/T_c$, reaches a maximum.

Discussion. – The present study proves for the first time the possibility of stochastic resonance in a realistic situation of multiple spike train transmission by the neuron. We chose not to oversimplify the model in a direction that could have facilitated the theoretical description of the stochastic resonance effect. On the contrary, we chose to preserve sufficient realism to the neuron and synaptic transmission modelling, especially for the essentially nonlinear stages that are introduced in signal transmission by these processes, as conveyed by eqs. (1), (2) and (3). With plausible numerical values for the parameters, the present treatment also authorizes both qualitative and quantitative interpretations. In such a context, strategies previously applied to the theoretical description of stochastic resonance do not seem to directly transpose here, in the presence of multiple neural nonlinearities and the transmission of trains of pulses.

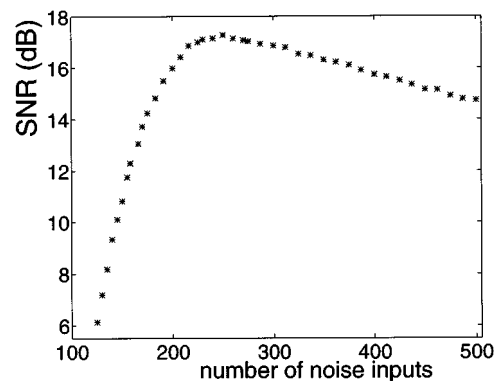


Fig. 3. – Output signal-to-noise ratio SNR as a function of the number N_n of noise input spike trains applied to the neuron.

A novel scheme of noise-enhanced signal transmission is shown here to be available with the basic mechanisms of neuronal response. The proposed scheme assigns, to noise trains produced by spontaneous random neuron spiking, a useful role in neural information processing, by improving the transmission of small coherent signals. Previous stochastic resonance experiments in neurons, as reported in the introduction, have mainly used external (environmental) noise. Internal noise originating in random fluctuations in the neuron is difficult to control [15]. The present scheme considers another source of internal noise, with the spontaneous random spiking of presynaptic neurons, which appears as a much more controllable internal noise source for a neural system to exploit, for signal transmission enhancement through stochastic resonance. Whether this scheme is actually used under this form by actual neurons is still an unproven matter, which requires experimental examination. Without further evidence, the present study demonstrates that such a scheme is at least authorized by the basic mechanisms of neural signal transmission, and that it may have important implications for information processing by neurons.

REFERENCES

- [1] NICOLIS C., *Tellus*, **34** (1982) 1.
- [2] BENZI R., PARISI G., SUTERA A. and VULPIANI A., *Tellus*, **34** (1982) 10.
- [3] MOSS F., BULSARA A. and SHLESINGER M. F. (Editors), *Proceedings of the NATO Advanced Research Workshop on Stochastic Resonances in Physics and Biology*, *J. Stat. Phys.*, **70** (1993) 1.
- [4] WIESENFELD K. and MOSS F., *Nature*, **375** (1995) 33.
- [5] LONGTIN A., *J. Stat. Phys.*, **70** (1993) 309.
- [6] LONGTIN A., BULSARA A., PIERSON D. and MOSS F., *Biol. Cybern.*, **70** (1994) 569.
- [7] WIESENFELD K., PIERSON D., PANTAZELOU E., DAMES C. and MOSS F., *Phys. Rev. Lett.*, **72** (1994) 2125.
- [8] JUNG P., *Phys. Rev. E*, **50** (1994) 2513.
- [9] GINGL Z., KISS L. B. and MOSS F., *Europhys. Lett.*, **29** (1995) 191.
- [10] DOUGLASS J. V., WILKENS L., PANTAZELOU E. and MOSS F., *Nature*, **365** (1993) 337.
- [11] LEVIN J. E. and MILLER J. P., *Nature*, **380** (1996) 165.
- [12] STEMMLER M., USHER M. and NIEBUR E., *Science*, **269** (1995) 1877.
- [13] CHAPEAU-BLONDEAU F., GODIVIER X. and CHAMBET N., *Phys. Rev. E*, **53** (1996) 1273.
- [14] CHAPEAU-BLONDEAU F. and CHAMBET N., *Neural Computation*, **7** (1995) 713.
- [15] PANTAZELOU E., DAMES C., MOSS F., DOUGLASS J. and WILKENS L., *Int. J. Bifurcation Chaos*, **5** (1995) 101.